THE ROLE OF ECOLOGY IN THE SPECIES EVALUATION OF THE GENUS *AFRONURUS* LESTAGE (HEPTAGENIIDAE) IN SOUTH AFRICA

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INTRODUCTION

This paper has largely been the outcome of a hydrobiological investigation of the Umgeni River System, Natal, South Africa, sponsored by the Town and Regional Planning Commission of Natal in association with the National Institute for Water Research of the Scientific and Industrial Research, Pretoria.

Within the framework of the broad objective laid down namely to protect the quality of the water resources of the Umgeni River Basin for domestic, agricultural, industrial and other uses, and at the same time to collect the basic data necessary for the formulation of stream and effluent standards, a program of investigation was worked out which also included a general ecological survey of the main Umgeni River and of its major tributaries (Fig. 1). During the course of this part of the survey, nearly a thousand individual samples of the aquatic macro-invertebrate fauna were collected over a period of two years at the various sampling localities, sorted, counted and identified as far as possible. In this way it was possible to obtain a picture of the fauna of a relatively clean and unpolluted river (and of its tributaries), from its source, at an altitude of over 6,000 ft. (1,829 m) to the Indian Ocean, a distance of 140-145 river miles (233-241 km).

Although a detailed investigation was made on the ecology of the macro-invertebrate fauna of several habitat types (Table 3) in the Umgeni River Basin the discussion in this paper will be mainly confined to the Ephemeropteran fauna of the stony bottom habitats. Some of the main reasons for the selection of the Ephemeroptera are the following :

1. The mayflies were found to be the dominant group (numerically and per biomass) amongst the macro-invertebrates of the unpolluted streams in the Umgeni Basin.
2. The stony bottom habitats provided a reliable picture of the habitat selection of the fauna, in this case the Ephemeroptera, from stagnant water conditions to the fastest current types encountered in streams. In this way, it was possible to obtain a representative cross section picture of the distribution of the stony bottom fauna at a specific sampling locality (ALLEN, 1951; HARRISON & ELSWORTH, 1958; CHUTTER, 1963).
3. The mayfly fauna was found to be amongst the organisms most sensitive to river pollution (SCHOONBEE, 1963a-c; SCHOONBEE & KEMP, 1963).

Only conditions of the fauna in the clean, unpolluted streams of the main Umgeni River will be discussed here.

More than 40 different species of mayflies were encountered in the Umgeni River Basin of which 35 were found in the main river alone. In order to falilitate the discussion on the ecology of the fauna a brief description of the Umgeni River and of some of its physical characteristics is given below.

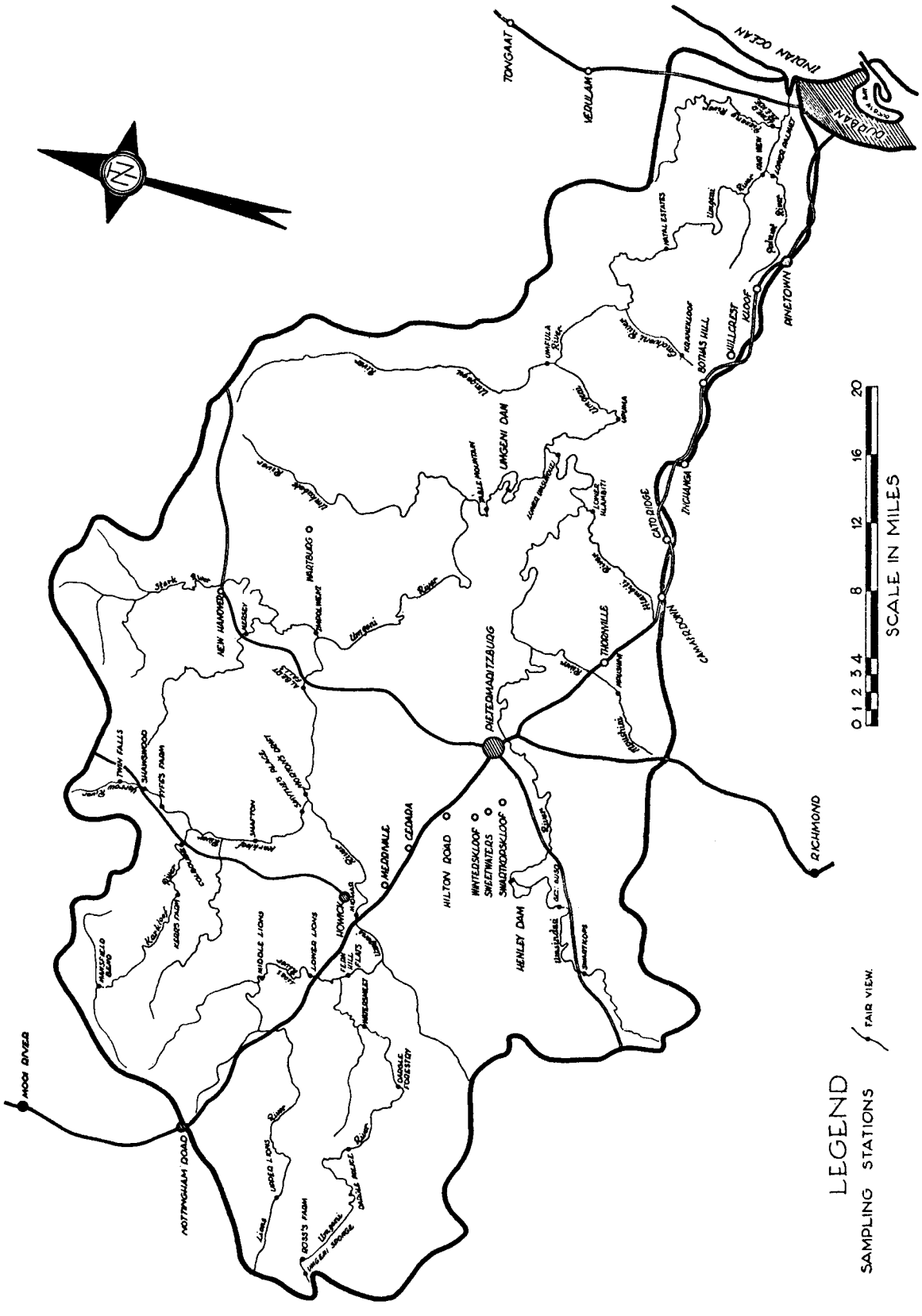

FIGURE 1. Sampling stations of the Umgeni River System.

General Description of the Umgeni River

The Umgeni River originates in a large vlei, called the Umgeni Sponge, at an elevation of just over 6000 feet, approximately 15 miles short of the Drakensberg Range. Unlike most other river systems such as, for instance, the Great Berg River in the Easter Cape (Harrison and Elsworth, 1958), the Umgeni River at its headwater flows through open rolling country, whilst it traverses in its lower 10-15 miles the deeply dissected terrain, namely the Valley of a Thousand Hills, an area where the river has incised itself profoundly, thereby creating deep and narrow gorges. In its lower 5-10 miles from the sea, a short flood plain exists. Here the numerous stony rapids are replaced by a wide sandy bed. The Umgeni River enters the Indian Ocean to the north of Durban Harbour, having traversed approximately 145 miles from source to mouth.

Physical zonation

Like most Natal rivers, the Umgeni has a steplike profile (Fig. 2) which is mainly determined by the monoclinal deformations of Natal (King and King, 1959) and assisted by erosion resistant dolorite sills, above which the river profile tends to flatten out only to regain its steep gradient below the water falls created by these sills. The presence of these dolorite intrusions cause a series of miniature profiles within the larger profile of the river, each with its own components of torrential and slower flowing regions. The fauna in streams are adapted to the various habitat types (Allen, 1951; Harrison and Elsworth, 1958; Chutter, 1963; Schoonbee, 1964) which are dependant upon variation in stream velocities. Also, since authors such as Harrison and Elsworth (1958), Oliff (1960) and Allanson (1961) found some correlation between the physical zonation of the river (see below) and the distribution of the fauna over the length of these rivers, it was decided, in addition to habitat studies, to find out whether the same conditions also prevail for the fauna in the Umgeni River Basin.

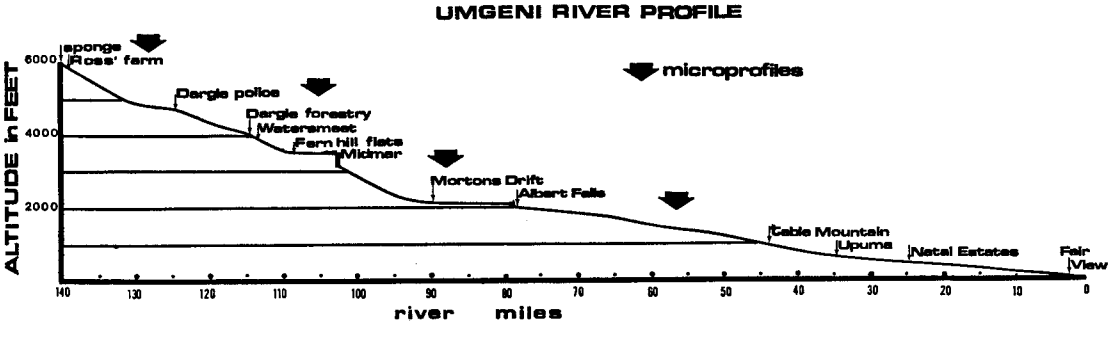

Figure 2. Umgeni River profile.

In Table I the physical zonation is represented for the Tugela River (Oliff, 1960), Great Berg River (Harrison and Elsworth, 9158) and the Jukskei River (Allanson, 1961). Of these, the Tugela and Great Berg Rivers show a similar physical zonation with both rivers having a source zone followed by a waterfall, mountain torrent and foothill torrent zone. The latter is subdivided by Oliff into an upper and lower stony run zone. In both systems a

foothill soft bottom zone precedes a rejuvenated river zone which in turn is replaced by a sand bed zone (called a flood plain zone by HARRISON and ELSWORTH) before the rivers reach the estuaries.

Table 1

Physical zonation of the Tugela River (Natal), Great Berg River (Cape) and Jukskei River (Transvaal)

River	*Tugela River* OLIFF, 1960)	*Great Berg River* (HARRISON & ELSWORTH, 1958)	*Jukskei-Crocodile River* (ALLANSON, 1960)
Physical zones	Source zone	Sponges	—
	Waterfall zone	Cliff waterfalls	—
	Mountain torrent zone	Mountain torrent zone	—
	Foothill torrent zone	Foothill stony run zone (upper) Foothill stony run zone (lower)	Upper reach Middle reach Lower reach
	Foothill sand bed zone	Foothill soft bottom zone	—
	Rejuvenated river zone	River rejuvenation (Piquetberg, St. 18)	—
	Valley sandbed zone	Flood Plain zone	—
	Estuarine zone	The Estuary	—

Table 2

Physical zonation of the Umgeni River, Natal

River Zone Types	*Microprofiles Within the Umgent River Profile*							
	1.		2.		3.		4.	
	Zone Area	*Altitude**	*Zone Area*	*Altitude**	*Zone Area*	*Altitude**	*Zone Area*	*Altitude**
Source zone	Umgeni sponge	6500+	—	—	—	—	—	—
Waterfall zone	—	—	—	—	—	—	—	—
Mountain torrent zone	Umgeni sponge - Ross' Farm	6000-6500	Dargle Falls - Dargle Forestry	4000-3300	Howick Falls - Mortons Drift	2700-2300	Immediately Below Albert Falls	2000-2100
Foothill torrent zone	Above Dargle Falls	4200-4000	Watersmeet - Howick	3200-3000	Above and below Mortons Drift	2300	Below Albert Falls - Natal Estates	2000-2100
Foothill soft bottom zone	—	—	—	—	Immediately above Albert Falls	2100+	Natal Estates - Fair View	500- 10
Eustuarine zone	—	—	—	—	—	—	Umgeni Estuary	10- 0

* Altitude in feet.

** Not a true mountain torrent (there are no mountains), but gradient equivalent to mountain torrential conditions.

As mentioned, the profile of the Umgeni River (Table 2, Fig. 2) is largely determined by doloritic sills which lay across the path of the river at places like Dargle, Howick and Albert Falls, but similar physical components as those used in the zonation of the Tugela and Great Berg Rivers also exist there (Table 2). A closer look at Figure I shows that the various physical zones can, as a result of the doloritic intrusions, be further subdivided into microprofiles (Table 2), each with a repetition of some of the components of the physical zones present in the Tugela and Great Berg Rivers respectively (Table 1).

Faunal Sampling Techniques

Various sampling devices have been developed and used by different research workers on problems of stream productivity (NEEDHAM, 1934; IDE, 1940; SPRULES, 1947). However, since the introduction of the square foot stream bottom sampler (SURBER, 1937; DAVIS, 1938), it has gained in popularity among research workers and has been widely used in the quantitative studies of stream bottom fauna in various contries as well as in Southern Africa (MACIOLEK and NEEDHAM, 1957; HARRISON and ELSWORTH, 1958; OLIFF, 1960; ALLANSON, 1961; CHUTTER, 1963).

Table 3

Habitat types sampled during the Umgeni River survey

Habitat	*Water Types sampled*
Marginal Vegetation	1. trailing in the current. 2. standing water.
Aquatic Vegetation	1. in slow current. 2. in fast current.
Stony Bottom	1. Back waters. 2. Pools. 3. Flats. 4. Runs. 5. Stickles. 6. Cascades.
Soft Bottom	1. Gravel. 2. Sand. 3. Mud.

A square foot (0.093 m^2) stream bottom Surber sampler and a handnet were largely employed in the faunal surveys under consideration. Both the handnet, which had a brass ring of 16 inches (40.6 cm) diameter, and the Surber sampler had bags of silk grit gauze of 25 meshes to the centimetre (64/inch). Quantitative stream bottom samples comprised 2-3 square foot Surber collections (0.186-0.279 m^2) which covered the different habitats at each site.

Habitat Types Sampled

Where it was possible, the following stream bottom habitats (= water types of Allen, 1951) were sampled. The current speeds and water depths at each habitat type in the Umgeni Basin roughly correspond with the findings of Harrison and Elsworth (1958).

The stony bottom water types

1. *Back waters* : "Sheltered parts of the stream, out of the main current ....." (Harrison and Elsworth, 1958, p. 136).

Usually these are less than six inches (± 15 cm) deep and are covered with detritus. The temperatures fluctuate much more than they do in any of the other water types during the different periods of the day.

2. *Pools* : "Water of considerable depth for the size of the stream, current generally slight, and the flow smooth apart from a small turbulent area at the head of some pools." (Allen).

"Current speed-under one foot per second; depth-over eighteen inches" (Harrison and Elsworth).

The pools sampled in the Umgeni River generally exceeded depths of 2 feet (± 61 cm). At Ross Farm, below the Sponge, for instance, a few pools sampled reached a depth of 3 feet (± 91.0 cm).

3. *Flats* : "Water of a slight to moderate current and generally smooth flow, but of less depth than in pools" (Allen).

"Current — under one foot per second; depth — under eighteen inches» (Harrison and Elsworth).

The flats sampled in the Umgeni River never exceeded one foot (± 30 cm) in depth whilst the maximum current speed, at times, exceeded 1 foot/second (= 30 cm./sec.).

4. *Runs* : "Water of moderate to rapid current and fairly deep, flow usually turbulent. In such places the stream is usually of less than average width" (allen).

"Current — over one foot per second; depth — over one foot, runs in sandy areas are shallower.» (Harrison and Elsworth.)

5. *Stickles* : "Shallow water with a rapid current and usually broken flow. Such conditions are often described as 'ripples', 'rapids', or 'riffles'" (Allen).

"Current — over one foot per second; depth — under one foot. The same proportion might be a run in the wet season and a stickle in the dry season." (Harrison and Elsworth).

Where no clear cut distinction could be made between runs and stickles, such samples were classified under "Runs and Stickles". These are discussed separately in the text.

6. *Cascades* : "Water in which a steep gradient, combined with a bed of stones or rocks large in proportion to the size of the stream, produces a very irregular flow, often with some white water." (Allen).

"Cascades and small waterfalls only occurred where streams were running down mountain slopes and valleys. Here current speeds were over 2.5 feet per second, and depth very variable but usually between four and eighteen inches." (Harrison and Elsworth).

The current speeds in cascades such as Ross' Farm and Albert Falls usually exceeded 2.5 feet/second (76.2 cm/sec.), averaging 2.75 feet/second (83.8 cm/sec.). The conditions otherwise resembled those described by Allen (1951) and Harrison and Elsworth (1958).

The Habitat Selection of the Stony Bottom Ephemeroptera

In Tables 4-9, the number of samples (N) obtained for each species include all the samples taken from all the main Umgeni River localities (Fig. 1) falling within a particular stretch of the river where such a species occurs, irrespective of its percentage incidence and numerical importance at any of the localities concerned. If, for example, *Baetis harrisoni* occurs in the Umgeni River at Ross' Farm, Dargle Forestry and Midmar (Figs. 1, 2), but was not collected at the other localities between these stations at Dargle Police Station, Watersmeet and Fern Hill Flats, this species was nevertheless considered as being potentially present in all the samples from all the habitats at these localities. Such samples are therefore included with those in which this species was actually recorded. The values in the "% pos." column (Tables 4-9) for each habitat are then based on the actual number of positive samples out of the total number of theoretically positive samples. Figures in the "% pos." column, therefore, roughly reflect the occurrence frequency of each species in a particular habitat. When considering the habitat selection of the stony bottom Ephemeroptera, certain families, represented by a few species only, are grouped together in some of Tables 4-9, merely for the sake of convenience.

Table 4

Habitat distribution of the Oligoneuriidae and Prosopistomatidae
[N = number of samples; $\bar{x}$ = mean number of specimens per sample; % pos. = the percentage of samples in which the species was found.]

Habitat	*Species*											
	Oligoneuriopsis lawrencei			*Elassoneuria trimeniana*			*Prosopistoma* sp.			*Prosopistoma crassi*		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	—	—	—	—	—	—	1	—	—	—	—	—
Pools	18	—	—	4	—	—	12	0.08	16.7	5	1.64	40.0
Flats	11	0.03	9.1	16	0.2	25.0	21	0.28	19.1	16	0.03	6.3
Runs	21	0.17	9.5	17	0.04	11.8	28	0.20	32.1	13	—	—
Runs and Stickles	10	0.19	20.0	21	0.28	19.1	20	0.08	30.0	16	0.18	25.0
Stickles	15	0.79	26.7	16	0.09	12.5	19	0.04	10.5	16	0.04	12.5
Cascades	3	—	—	3	0.13	33.3	3	—	—	3	—	—

Oligoneuriidae

Although represented by two genera viz. *Oligoneuriopsis* and *Elassoneuria*, the nymphs of the two species *O. lawrencei* and *E. trimeniana* not only are morphologically very similar but also occupy the same habitat types. In both species the nymphs usually "cluster" under stones. In

contrast to species such as those of the genus *Afronurus*, nymphs of both species appeared to be intolerant of stagnant waters. *O. lawrencei*, for instance, was not recorded from any one of 18 samples collected from pools (Table 4). The species furthermore occurred in increasingly larger numbers in habitats with increased current speeds (flats stickles, Table 4) which in turn coincided with increases in the percentage sample incidences (% pos., Table 4). *Elassoneuria trimeniana* appears to be slightly less specific in habitat preference, being present in all the habitat types except pools (stony back waters were not sampled). The largest average percentage for this species was recorded from the stony runs and stickles.

Prosopistomatidae

Even though their body shape may suggest an adaptation to swift current conditions, the nymphs of *Prosopistoma* were most common in slow and moderate current habitat types, i.e. pools, flats and runs (Table 4). *Prosopistoma* sp. was mainly found in stony flats and runs but also occurred in pools. Nymphs of *P. crassi*, which are much more dorsoventrally depressed compared with *Prosopistoma* sp., were more common in the slow flowing or stagnant waters of pools (Table 4). Both species live under stones.

Tricorythidae

Neurocaenis discolor as a rule occurs under stones. In the Umgeni River it invaded all stony bottom habitats from virtually stagnant waters in pools to the fastest current (Table 5). The nymphs appeared to prefer the moderate current of the stony flats and runs to the faster current conditions of the stickles and cascades. The smallest individual and average numbers obtained for this species were those from the back waters and pools (Table 5).

Table 5

Habitat distribution of the Tricorythidae, Caenidae, Polymitarcidae and Ephemerellidae

Habitat	*Species*											
	Neurocaenis discolor			*Caenis* spp.			*Ephoron savigni*			*Lithogloea* near *harrisoni*		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	2	1.85	50.0	1	1.8	100.0	—	—	—	—	—	—
Pools	22	1.94	60.0	15	1.2	53.3	1	—	—	4	—	—
Flats	15	5.08	63.6	23	1.4	69.6	11	0.04	18.2	12	0.20	8.3
Runs	27	5.70	70.4	28	1.1	53.6	7	0.1	14.3	10	—	—
Runs and Stickles	26	4.24	57.7	23	1.3	69.6	7	0.03	14.3	11	—	—
Stickles	22	4.12	72.7	23	1.2	39.1	9	—	—	10	0.08	10.0
Cascades	7	2.67	57.1	6	0.2	50.0	3	0.26	33.3	3	—	—

Caenidae

At least five species could be recognized from the nymphs alone, some of which definitely appeared to favour slow current conditions. *Caenis* sp. 4, for instance, usually were frequent in stagnant waters and amongst the marginal vegetation. In Table 5, the five species are, however, grouped together. Species of *Caenis* occurred in all habitats with the lowest average percentage incidences in the cascades. If sorted to the species and correlated with adults, some species may certainly prove to be tolerant of the fast current conditions in runs, stickles and cascades.

Polymitarcidae

This family is represented in the Umgeni River by one species only, namely *Ephoron savigni*. It occurred amongst small stones or in gravelly types of stream bottom at Midmar and Albert Falls. The nymphs favoured habitats with moderate to fast current conditions (Table 5). The largest average percentage incidence was registered from the cascade.

Ephemerellidae

CRASS (1947) claims that he found an ephemerellid at the Yarrow Falls (= Twin Falls, Fig. 2) on the Yarrow River the description of which (personal communications) fits a similar species collected during the Umgeni River survey at Impolweni on the Sterk River (SCHOONBEE, unpublished data). A nymph of this particular, or, a closely related species was provisionally placed by DEMOULIN (1959) in the new genus and new species of *Machadorythus palanquim*.

The recovery of *Lithogloea* near *harrisoni* from the Umgeni River system represented the first record of this genus in Natal. *Lithogloea* near *harrisoni* was not very common and apart from its presence in the stony bottom habitats, it was also collected from the trailing marginal vegatation at Table Mountain, and from the aquatic vegetation *Hydrostachys natalensis* at Morton's Drift. In the stony bottom habitats it mainly occurred in moderate current conditions of the stony flats.

Leptophlebiidae

Of the five species of the leptophlebiid family found in the main Umgeni River viz. *Castanophlebia calida*, *Aprionyx tricuspidatus*, *Adenophlebia auriculata A. sylvatica*, and *Choroterpes (Euthraulus)? bugandensis*, only the nymphs of *Castanophlebia calida* appeared to favour swift current conditions (Table 6). The latter species, however, also occurred in pools where the water was virtually stagnant. *A. tricuspidatus* was not very common in the Umgeni River and, furthermore, was very much restricted in its habitat preference. Its nymphs were found only in habitats with slow or moderate current speeds such as the stony flats and, in some instances (Emolweni Tributary; unpublished data), amongst the marginal vegetation in the slow current. The nymphs of *A. sylvatica* had their highest average percentage incidences in the flats and pools. Compared with *A. sylvatica*, *A. auriculata* nymphs appeared to be capable of invading more habitat types. Even so, this species, like *A. sylvatica*, was more abundant in the pools and flats (Table 6). Similarly, *Choroterpes (Euthraulus)? bugandensis* also selected the pools and stony flats, being absent only from the stony back waters and cascades.

Table 6

Habitat distribution of the Leptophlebiidae

Habitat	*Species*														
	Castanophlebia calida			*Aprionyx tricuspidatus*			*Adenophlebia sylvatica*			*Adenophlebia auriculata*			*Choroterpes (E.) ? bugandensis*		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	1	—	—	—	—	—	2	—	—	2	1.40	50.0	2	—	—
Pools	3	2.23	33.3	3	—	—	7	1.61	14.2	7	3.67	28.6	15	2.96	60.0
Flats	2	3.30	100.0	2	2.95	100.0	8	2.80	50.0	11	2.94	45.5	15	2.96	60.0
Runs	—	—	—	—	—	—	8	—	—	11	2.43	36.4	24	0.95	45.8
Runs and Stickles	3	3.10	66.7	3	—	—	3	—	—	4	0.90	50.0	21	0.72	42.9
Stickles	4	4.15	50.0	4	—	—	6	0.15	16.7	11	0.16	36.4	20	0.74	35.0
Cascades	—	p*	—	3	—	—	3	—	—	3	—	—	3	—	—

p* Present but not recorded from survey sample.

Baetidae

Two species of *Baetis* of the *Acentrilla* type were encountered, namely *B. monticola* and *B. natalensis*. Both distinctly favoured fast current conditions, having their highest average percentage incidence in the stony stickles (Table 7), and their average percentage numbers per sample decreasing successively in the slower current habitats. Of interest is the downstream distribution in the Umgeni River of *B. natalensis* which became progressively more restricted to one particular type of microhabitat where a thin film of water skimmed rapidly over stone and rock surfaces in the stickles and cascades. This contrasts sharply with the presence of *B. natalensis* nymphs in most stony bottom habitats at or near the headwater region of the Umgeni River. (This species with its very small and rounded gills appeared to be sensitive to low concentrations of dissolved oxygen.)

The two species of *Pseudocloeon* showed marked differences with respect to habitat preferences. *Pseudocloeon inzingae*, for instance, favoured the slow current or stagnant waters of the pools and back waters (Table 7) whereas, *P. maculosum* largely occurred in the faster current, being, on the average, most common in the stony stickles. The percentage of samples in which it actually occurred, consequently, reflects an increase of this species from the slower to the faster current habitats.

Baetis harrisoni was, numerically, the most important mayfly species in the Umgeni River. It invaded most habitats but occurred in larger numbers in moderate to fast current habitats such as the stony flats, runs and stickles (Table 7). *Baetis glaucus*, although not as prominent, numerically, as *B. harrisoni*, had a habitat preference very similar to the latter. The nymphs of *B. cataractae*, on the other hand, distinctly favoured very swift currents. Where this species

was found in moderate current habitats, the nymphs mainly comprised penultimate or final instars. The ventral gill baetid (= Baetidae nymph A, KIMMINS, 1955) occurred in all habitats sampled (back waters were not sampled). Its nymphs were more common in the runs and stickles where they were found to cling to the steep surfaces of rocks and stones. In captivity these nymphs were found to die soon unless a current was created against an object where they usually attached themselves, facing the current.

Table 7

Habitat distribution of the Baetidae : the genera Baetis and Pseudocloeon

Habitat	*Species*																							
	Baetis monticola			*Pseudocloeon inzingae*			*Baetis cataractae*			*Baetis natalensis*			*Baetis harrisoni*			*Baetis glaucus*			*Pseudocloeon maculosum*			*Baetid with ventral gills*		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	1	—	—	1	7.2	100.0	2	—	—	2	0.25	50.0	2	0.9	100.0	1	—	—	—	—	—	—	—	—
Pools	3	1.03	66.7	3	10.37	100.0	7	—	—	14	0.07	14.3	15	8.1	73.3	12	0.12	8.3	5	0.06	20.0	4	0.30	25.0
Flats	2	—	—	1	—	—	7	0.04	14.3	20	1.48	45.0	22	13.9	90.9	21	1.26	38.1	16	0.17	18.8	12	0.08	8.3
Runs	—	—	—	—	—	—	7	—	—	22	1.22	27.3	28	14.8	85.7	18	1.33	33.3	13	0.09	15.4	10	0.07	10.0
Runs & Stickles	2	3.55	50.0	2	—	—	2	—	—	17	2.35	58.8	28	12.0	76.0	12	2.48	47.8	16	0.16	31.3	11	0.16	9.1
Stickles	3	9.16	100.0	4	—	—	4	0.25	50.0	21	5.52	66.7	23	14.0	95.7	11	1.22	42.1	16	0.24	37.5	10	0.12	10.0
Cascades	—	—	—	3	—	—	3	—	—	5	2.57	83.3	5	10.1	100.0	3	0.80	66.2	3	0.20	66.7	3	0.10	33.3

Species of *Centroptilum* (Table 8) which are mainly distributed in slow current habitats include *Centroptilum* near *excisum*, *C. sudafricanum*, *C. indusii*, *Centroptilum sp.* 2, *Centroptilum* sp. 3 and *C. medium*. Of these, *C. sudafricanum* is the most common species, occurring in all stony bottom habitats, with *Centroptilum* near *excisum* being restricted to the stony back waters, pools and flats. *C. parvum*, which never featured prominently compared with species such as *C. sudafrisanum*, appeared to be more common in the stony runs and stickles.

Centroptiloides bifasciata, *Centoptilum varium*, *C. flavum* and *Centroptilum* sp. 1 distinctly favoured the faster current habitats. Of these, *Centroptiloides bifasciata* and *Centroptilum* sp. 1 are stony clingers, both species occurring mainly on rocks and stones where the current plunged over large boulders in the cascades and stickles respectively. *Centroptilum varium*, like *Baetis cataractae*, preferred microhabitats similar to those where *Baetis natalensis* occurred, i.e. where thin films of water flowed rapidly over rock surfaces in the stream.

Table 8

Habitat distribution of the Baetidae : the genera Centroptilum and Centroptiloides

Habitat	*Species of Centroptilum and Centroptiloides*																	
	Centroptilum near *excisum*			*Centroptilum sudafricanum*			*Centroptilum parvum*			*Centroptilum* sp. 2			*Centroptilum indusii*			*Centroptilum* sp. 3		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	1	11.7	100.0	2	40.5	100.0	1	0.90	100.0	2	0.90	50.0	2	—	—	1	—	—
Pools	3	1.7	66.7	5	9.6	58.3	8	0.50	25.0	15	1.44	40.0	14	0.58	28.6	8	2.51	37.5
Flats	3	2.4	66.7	20	5.9	55.0	16	0.02	6.3	18	0.12	16.7	22	2.73	22.7	15	0.17	13.3
Runs	—	—	—	20	3.9	55.0	22	0.87	13.6	25	0.10	20.0	27	0.13	18.5	21	0.28	19.1
Runs and Stickles	3	—	—	16	0.5	18.0	11	0.53	18.2	21	0.07	14.3	22	0.03	4.5	11	0.18	18.2
Stickles	4	—	—	21	0.8	38.0	12	0.70	25.0	18	<0.01	5.6	22	0.11	9.1	11	0.04	9.1
Cascades	3	—	—	6	0.1	16.7	3	—	—	6	0.08	16.7	6	—	—	3	0.37	66.7

Table 8 (*continued*)

Habitat distribution of the Baetidae : the genera Centroptilum and Centroptiloides

Habitat	*Species of Centroptilum and Centroptiloides*														
	Centroptilum medium			*Centroptiloides bifasciata*			*Centroptilum varium*			*Centroptilum flavum*			*Centroptilum sp.* 1		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	1	—	—	2	—	—	2	—	—	—	—	—	—	—	—
Pools	12	3.48	41.7	15	0.02	6.7	15	—	—	—	—	—	4	—	—
Flats	21	0.21	9.5	22	0.06	13.6	13	0.09	15.4	7	—	—	5	—	—
Runs	28	0.35	10.7	28	0.04	17.9	24	0.02	8.3	4	—	—	6	0.22	16.7
Runs & Stickles	20	0.05	10.0	22	0.15	22.7	22	0.35	27.2	2	<0.01	50.0	11	0.63	27.3
Stickles	19	0.44	21.1	23	0.24	26.1	20	0.74	35.0	3	—	—	7	0.71	28.6
Cascades	3	0.03	33.3	6	0.22	8.3	3	—	—	3	—	—	—	—	—

Heptageniidae

Altogether four species were recognized (Table 9) of which *Afronurus oliffi* predominated in slow current habitats. It was absent from the stony stickles and cascades and had its highest individual and average percentage incidence in pools.

Table 9

Habitat distribution of the Heptageniidae

Habitat	*Species*											
	Afronurus oliffi			*Afronurus barnardi*			*Afronurus scotti*			*Afronurus peringueyi*		
	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.	N	$\bar{x}$	% pos.
Back Waters	1	0.9	100.0	2	—	—	2	0.9	50.0	—	—	—
Pools	3	6.1	66.7	10	0.99	20.0	12	8.22	66.7	4	16.6	50.0
Flats	1	—	—	10	0.29	30.0	23	4.04	73.9	12	0.43	25.0
Runs	—	—	—	17	0.32	17.7	26	4.49	57.7	10	0.76	10.0
Runs and Stickles	2	1.4	50.0	12	0.19	33.3	22	0.76	59.1	11	0.34	9.1
Stickles	4	—	—	12	0.36	41.7	23	2.93	73.9	10	0.13	20.0
Cascades	3	—	—	3	—	—	6	1.27	50.0	3	0.27	33.3

Afronurus barnardi was recorded from all habitats excepts the stony back waters and cascades. It was fairly common in the moderately fast current habitats such as the stony flats, runs and stickles but, like *A. oliffi*, had its highest average percentage incidence in pools.

Afronurus scotti was, numerically, the most abundant species of the stony bottom Heptageniidae. It occurred in all habitats but was most common in the stony flats, runs and stickles. The smallest percentage incidences were recorded from the stony back waters and cascades. This species distinctly gave preference to pools.

Afronurus peringueyi was most common in pools, comprising an average incidence of 16.6% (Table 9). Apart from the stony back waters, which were not samples in the zone of occurrence of *A. peringueyi* ,this species invaded all other habitat types.

From the fore-going it is clear that all four *Afronurus* species distinctly favoured pool-like conditions. These findings somewhat disagree with those of Crass (1947) who found *Afronurus* to be a specially adapted swift water form, "... distinctly intolerant of still waters" (p. 41). In fact, its strongly dorsoventrally flattened body shape does not appear to be an adaptation to swift current, as was previously suspected, but rather to life under stones and in crevices. This would be in agreement with the findings of Dodds and Hisaw (1924) who, in their studies on the adaptation of mayfly nymphs to swift streams, concludes that the flattened bodies of *Ecdyurus* and *Drunella* probably enabled these species to creep into narrow crevices under stones.

Compared with other mayfly genera the nymphs of *Afronurus* have large eyes. They appear to be sensitive to light intensity which may perhaps in part explain their commonness in pools where much of the effective light penetration decrease with increasing depth of the water. In captivity, nymphs were found to leave the stones at night during the period of ecdysis. All four species are very sensitive to stream disturbance and are amongst the first Ephemeroptera to disappear from the fauna when such conditions arise (SCHOONBEE & KEMP, 1963). Their presence in streams can therefore always be taken as indicative of clean unpolluted waters.

THE LONGITUDINAL (DOWNSTREAM) DISTRIBUTION OF THE STONY BOTTOM EPHEMEROPTERA IN THE UMGENI RIVER

For the purpose of illustrating the distribution of the stony bottom Ephemeroptera in the Umgeni River as one proceeds downstream from Ross' Farm, the various species are listed against their respective sampling stations and physical zones. As in the preceding section on the habitat selection of the stony bottom mayflies, species of different families are grouped together in some of the tables. In Tables 10-15, however, the species were arranged according to their downstream distribution, those confined to the Ross' Farm locality, being placed first, followed successively by other species which predominated in consecutive stretches lower down in the river. In Tables 10-15, the average percentage incidences ($\bar{x}$) and the percentage sample occurrence[1] (% pos.) for each locality are based on all samples from such particular locality.

Table 10

Longitudinal (downstream) distribution of the Heptageniidae

Physical zone	*Microprofile*	*Sampling Locality*	N	*Species*							
				Afronurus oliffi		*Afronurus barnardi*		*Afronurus scotti*		*Afronurus peringueyi*	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	—	—	—	—	—	—	—	—
Mountain Torrent	1	Ross' Farm	14	1.6	28.6	0.5	28.6	0.15	14.3	—	—
Foothill Torrent	1	Dargle Police Station	2	—	—	—	—	2.55	100.0	—	—
Mountain Torrent	2	Dargle Forestry	20	—	—	0.55	15.0	8.18	90.0	—	—
Foothill Torrent	2	Watersmeet	6	—	—	—	—	p*	—	—	—
		Fern Hill Flats	7	—	—	—	—	0.24	28.6	—	—
Mountain Torrent	3	Midmar	11	—	—	0.54	54.5	4.22	81.8	—	—
		Morton's Drift	8	—	—	—	—	6.60	100.0	—	—
Mountain Torrent	4	Albert Falls	19	—	—	p*	—	14.95	89.5	0.63	21.1
Foothill Torrent	4	Table Mountain	14	—	—	—	—	3.64	64.3	4.98	35.7
		Upuma	17	—	—	—	—	0.28	52.9	0.19	17.7
Foothill Soft bottom	4	Natal Estates	2	—	—	—	—	—	—	—	—
		Fair View		No stony bottoms							

* present but not recorded from survey samples.

[1] Based on the number of positive samples for each species, and the total number of samples taken from each locality.

Certainly one of the most stricking features in the downstream distribution of the aquatic fauna in general and of the stony bottom Ephemeroptera in particular, was the existence, in communities, of more than one faunal association, each of which occupied and predominated in a particular stretch of the river. As an example of, and, also, as an introduction to the discussion of the longitudinal distribution of each of the faunal associations, the occurrence, in the river, of the four species of the heptageniid genus *Afronurus*, are dealt with first.

Heptageniidae

Most noteworthy of the distribution of the four species of *Afronurus* was the fact that even though all of them occupied similar habitats, each species predominated over different stretches of the river. *Afronurus oliffi*, for instance, was very much restricted to the head water region at Ross' Farm (Table 10), being absent at all the other downstream localities. *Afronurus barnardi*, on the other hand, although never numerous, had its highest average percentage incidences in the locatilies of the mountain and foothill torrent zones of microprofiles 1 and 2. It disappeared entirely from the fauna downstream from Albert Falls, where it was collected only during special extensive surveys. *Afronurus scotti*, in contrast to the abovementioned two species, was not only a numerically more important species, but successfully invaded all the physical zones of the river except the source and foothill soft bottom zones, having its highest average percentage incidence at localities from Dargle Forestry downstream to Albert Falls. *Afronurus peringueyi* was mainly restricted to the mountain torrent zone of microprofile 4 below Albert Falls.

This difference in longitudinal distribution of the *Afronurus* species was of considerable value in the separation of *A. barnardi* and *A. peringueyi* which are so closely related morphologically that they could easily have been taken for the *forma minor* and *forma major* of a single species (c.f. BARNARD, 1932). Their predominance in different stretches of the river, however, dispelled all doubts as to the actual differences between the two species. This separation of the two species on the basis of their ecological distribution was subsequently confirmed by some clear cut morphological differences as well (SCHOONBEE, 1968). Of particular interest were the differences, between the species, in the averages of the ratio head width/length which, with the exception of *A. scotti*, declined in the same successional order as their downstream occurrence in the river. In the nymphs, the decline in this ratio furthermore coincided with a concordant decrease in the average numbers of algal rakers on the maxillae, which in turn can be correlated with the general downstream increase in algal growths. The head ratio of *A. harrisoni* from the mountain torrent zone in the Great Berg River is even higher than it is in *A. oliffi* from the upper foothill torrent in the Umgeni River. This seems to fall in line with the findings put forward above because the algal and diatom growths appeared to be much less in this zone of the Berg River than they are even in the foothill torrent of microprofile 2 of the Umgeni River.

The Oligoneuriidae and Prosopistomatidae

Although none of the four species under consideration were numerous, the following distributional tendencies were observed.

Oligoneuriopsis lawrencei occurred over four successive physical zones (Table II), having its highest average percentage incidences as well as percentage sample occurrence in the first and second foothill torrent and the mountain torrent zone 3. Compared with the distribution of the

four species of *Afronurus*, the pattern of distribution shown by *O. lawrencei*, although not recorded from Ross' Farm, roughly agrees with that of *Afronurus barnardi*.

Prosopistoma sp. had a comparatively wide range of distribution, occurring from Ross' Farm downstream as far as Upuma. Its average percentage incidence as well as its percentage incidence in samples revealed this species to be most common in the mountain torrent zones 3 and 4. Its outstretched longitudinal distribution suggests ecological preferences similar to those of *Afronurus scotti*.

Table 11

Longitudinal (downstream) distribution of the Oligoneuriidae and Prosopistomatidae

Physical zones	*Microprofile*	*Sampling localities*	N	*Species*							
				Oligoneuriopsis lawrencei		*Prosopistoma* sp.		*Elassoneuria trimeniana*		*Prosopistoma crassi*	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	—	—	—	—	—	—	—	—
Mountain Torrent	1	Ross' Farm	14	—	—	p*	—	—	—	—	—
Foothill Torrent	1	Dargle Police Station	2	0.9	50.0	0.15	50.0	—	—	—	—
Mountain Torrent	2	Dargle Forestry	20	—	—	0.11	10.0	—	—	—	—
Foothill Torrent	2	Watersmeet	6	0.13	33.3	0.05	16.6	—	—	—	—
		Fern Hill Flats	7	0.47	28.6	0.03	14.2	0.64	14.3	—	—
Mountain Torrent	3	Midmar	11	0.72	18.2	—	—	0.12	18.2	0.04	9.1
		Morton's Drift	8	—	—	0.16	37.5	—	—	0.04	12.5
Mountain Torrent	4	Albert Falls	19	0.01	5.3	0.14	31.6	0.11	21.1	p*	—
Foothill Torrent	4	Table Mountain	14	0.26	7.1	0.30	28.6	0.01	7.1	0.68	42.9
		Upuma	17	—	—	0.21	29.4	0.19	23.5	0.11	5.9
Foothill Soft Bottom	4	Natal Estates	2	—	—	—	—	0.15	50.0	—	—
		Fair View		No stony bottoms.							

* present but not recorded from survey samples.

The distribution of *Elassoneuria trimeniana* appears to be intermediate between that of *Afronurus scotti* and *A. peringueyi*. It can, however, be best compared with the distribution of *Afronurus scotti* since this species occurred from the foothill torrent zone 2 downstream as far as the foothill soft bottom zone 4. Unfortunately, its average incidence does not show any marked predominance in any part of the river.

Even though *Prosopistoma crassi* had a wider (upstream) distributional range than *Afronurus peringueyi*, the highest average numbers of *P. crassi* occurred in the mountain torrent zone 4, thus agreeing well with the distribution of *Afronurus peringueyi*.

The Tricorythidae, Caenidae, Polymitarcidae and Ephemerellidae

Numerically, *Neurocaenis discolor* was one of the most common species of mayflies in the Umgeni River, having, like *Afronurus scotti*, an extended range of longitudinal distribution (Table 12). The stretch of the river in which it had its highest average percentage incidence and percentage occurrence in samples showed a similarity to that of *Afronurus scotti*.

Table 12

Longitudinal (downstream) distribution of the Tricorythidae, Caenidae, Polymitarcidae and Ephemerellidae

Physical Zones	*Microprofile*	*Sampling Localities*	N	*Species*							
				Neurocaenis discolor		*Caenis* spp.		*Ephoron savigni*		*Lithogloea* near *harrisoni*	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	—	—	0.35	50.0	—	—	—	—
Mountain Torrent	1	Ross' Farm	14	1.86	50.0	2.19	57.1	—	—	—	—
Foothill Torrent	1	Dargle Police Station	2	8.05	100.0	2.10	50.0	—	—	—	—
Mountain Torrent	2	Dargle Forestry	20	6.04	80.0	0.96	55.0	—	—	—	—
Foothill Torrent	2	Watersmeet	6	8.10	83.3	0.27	33.3	—	—	—	—
		Fern Hill Flats	7	0.24	28.6	0.33	42.9	—	—	—	—
Mountain Torrent	3	Mismar	11	14.06	100.0	0.53	45.5	0.04	18.2	—	—
		Morton's Drift	8	4.50	87.5	0.26	37.5	—	—	p*	—
Mountain Torrent	4	Albert Falls	19	2.33	78.9	1.13	73.7	0.09	15.8	0.13	5.3
Foothill Torrent	4	Table Mountain	14	1.12	28.6	1.36	42.9	—	—	<0.01	7.1
		Upuma	17	2.81	41.2	2.34	76.5	—	—	0.05	5.9
Foothill Soft Bottom	4	Natal Estates Fair View	2	3.35	100.0	—	—	—	—	—	—
				No stony bottoms.							

* present in aquatic vegetation

The specimens of *Caenis* were not sorted to species and, consequently, are treated as a group (Table 12), which showed two peaks in average incidence, one in the mountain torrent zone and the foothill torrent zone I, and one in the mountain and foothill torrent zones 4. It is, however, not possible to state at this stage whether individual species were responsible for these peaks.

Lithogloea near *harrisoni* occurred in small numbers. Its distribution is very similar to that of *Afronurus peringueyi*, being mainly confined to the mountain torrent zone 4.

The Leptophebiidae

Of the five species of the stony bottom leptophlebiids encountered in the main river, at least two species were very much restricted to the head waters at Ross' Farm (Table 13). They are *Castanophlebia calida* and *Aprionyx tricuspidatus*. Both species were (also in the tributaries) found to be associated with *Afronurus oliffi* (SCHOONBEE, unpublished data). A third species *Adenophlebia sylvatica*, although having a slightly more extended longitudinal range of distribution than *Afronurus oliffi* (Table 13), had its largest average percentage incidences at the source and at Ross' Farm (mountain torrent zone I) and, consequently, can also be included with those Ephemeroptera which were confined to the headwaters of the river.

Table 13

Longitudinal (downstream) distribution of the Leptophlebiidae

Physical Zones	*Microprofile*	*Sampling Localities*	N	*Species*									
				Castanophlebia calida		*Aprionyx tricuspidatus*		*Adenophlebia sylvatica*		*Adenophlebia auriculata*		*Choroterpes (E.) ? bugandensis*	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	0.70	100.0	—	—	9.30	100.0	7.20	50.0	—	—
Mountain Torrent	1	Ross' Farm	14	2.56	46.7	0.37	12.5	1.06	20.0	1.47	20.0	0.64	35.7
Foothill Torrent	1	Dargle Police Station	2	—	—	—	—	—	—	0.45	100.0	0.45	100.0
Mountain Torrent	2	Dargle Forestry	20	—	—	—	—	0.01	10.0	2.29	35.0	2.74	60.0
Foothill Torrent	2	Watersmeet	6	—	—	—	—	—	—	—	—	0.13	16.7
		Fern Hill Flats	7	—	—	—	—	—	—	—	—	0.24	28.6
Mountain Torrent	3	Midmar	11	—	—	—	—	—	—	0.88	45.5	2.92	63.6
		Morton's Drift	8	—	—	—	—	—	—	—	—	2.45	62.5
Mountain Torrent	4	Albert Falls	19	—	—	—	—	—	—	—	—	3.60	89.5
Foothill Torrent	4	Table Mountain	14	—	—	—	—	—	—	—	—	1.12	28.6
		Upuma	17	—	—	—	—	—	—	—	—	0.39	41.2
Foothill Soft Bottom	4	Natal Estates Fair View	2	—	—	—	—	—	—	—	—	—	—
				No stony bottoms									

Adenophlebia auriculata had a distribution resembling that of *Afronurus barnardi*, being more common at the source but, in contrast to *Afronurus oliffi* and its associated fauna, it

extended downstream as far as Midmar (mountain torrent zone 3). The distributional range of *Choroterpes* (*Euthraulus*)? *bugandensis*, as well as its higher average percentage incidences in localities from the mountain torrent zone 2 downstream towards the upper part of the mountain torrent zone 4 (Table 13), suggest an ecological distribution similar to that of *Afronurus scotti*.

The Baetidae

Four species, which had longitudinal distributions similar to that of *Afronurus oliffi*, included *Pseudocloeon inzingae*, *Baetis cataractae*, *Baetis monticola* and *Centroptilum* near *excisum* (Tables 14-15), all of which were very much restricted in their longitudinal distribution. Mayfly species which predominated in the same stretch of the river as *Afronurus barnardi* included *Baetis natalensis*, *Centroptilum sudafricanum*, C. *parvum* and *Centroptilum* sp. 2. All these species numerically declined downstream from below the foothill torrent zone 1. Those baetids which best fitted the distributional pattern of *Afronurus scotti* included the species *Centroptilum medium*, *C. indusii*, *Centroptilum* sp. 3 and *Baetis harrisoni*. Species which were mainly confined to, or, had their highest average incidences in the mountain torrent zone 4 were *Baetis glaucus*, *Pseudocloeon maculosum*, a baetid with ventral abdominal gills and *Centroptilum* sp. I. *Centroptiloides bifasciata*, which never attained large average incidences anywhere in the river, nevertheless showed increases at localities between the mountain torrent zone 2 and the foothill soft bottom zone and in this respect should be placed with the group of mayflies associated with *Afronurus scotti*. *Centroptilum varium* which occurred in all zones downstream from Ross' Farm (mountain torrent zone 2), as far as the foothill torrent zone 4, showed increases in average percentage incidence in that part of the river from Midmar to Natal Estates. In this respect *Centroptilum varium* appeared to be virtually intermediate in distribution between the *Afronurus scotti* and *A. peringueyi* associations, sharing the extended longitudinal range of occurrence with the *Afronurus scotti* association, but, on the other hand, showing distinct average numerical increases in the lower mountain torrent zone of microprofile 3. Since the *Afronurus peringueyi* association was restricted and mainly confined to the rejuvenated river zone, *C. varium* is provisionally placed with the *Afronurus peringueyi* association. *Centroptilum flavum* was recorded in the main river from Albert Falls only, and is therefore also provisionally grouped with the *Afronurus peringueyi* association.

From the findings on the longitudinal (= downstream) distribution of the stony bottom Ephemeroptera in the Umgeni River, the following pattern evolved :

1. The faunal communities at most sampling localities comprised more than one association of stony bottom Ephemeroptera.
2. Each association is confined to, and predominates, in, one particular region or stretch of the river. Furthermore, the associations were found to overlap and to replace each other in an orderly sequence downstream, each intergrading with components of other associations which extended either upstream or downstream from those stretches in the river where they predominate.
3. Each association, although recognizable from the position it occupies in the river, contains species which extend beyond the range of the association and which can be regarded as being transitional in distribution between two successive associations.
4. The different associations are not necessarily confined to particular physical zones, but, in most instances, extend over more than one zone.

Table 14

Longitudinal (downstream) distribution of the Baetidae : the genera Baetis and Pseudocloeon

Physical Zones	*Microprofile*	*Sampling Localities*	N	*Species*															
				Baetis monticola		*Pseudocloeon inzingae*		*Baetis cataractae*		*Baetis natalensis*		*Baetis harrisoni*		*Baetis glaucus*		*Pseudocloeon maculosum*		*Baetid with ventral gills*	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	—	—	—	—	—	—	—	—	0.7	100.0	—	—	—	—	—	—
Mountain Torrent	1	Ross' Farm	14	2.69	42.9	2.74	28.6	0.07	14.3	6.80	71.6	9.9	100.0	—	—	—	—	—	—
Foothill Torrent	1	Dargle Police Station	2	—	—	—	—	—	—	1.65	100.0	20.8	100.0	0.50	50.0	—	—	—	—
Mountain Torrent	2	Dargle Forestry	20	—	—	—	—	0.02	5.0	5.07	65.0	25.9	95.0	0.09	15.0	—	—	—	—
Foothill Torrent	2	Watersmeet	6	—	—	—	—	—	—	0.42	33.0	15.4	83.3	—	—	—	—	—	—
		Fern Hill Flats	7	—	—	—	—	—	—	0.14	28.5	6.3	100.0	—	—	—	—	—	—
Mountain Torrent	3	Midmar	11	—	—	—	—	—	—	0.53	36.4	12.0	100.0	1.28	36.4	0.20	36.4	—	—
		Morton's Drift	8	—	—	—	—	—	—	2.10	62.5	13.0	87.5	0.68	37.5	0.38	25.0	—	—
Mountain Torrent	4	Albert Falls	19	—	—	—	—	—	—	0.17	21.1	14.6	84.2	1.26	42.1	0.18	31.6	0.02	5.3
Foothill Torrent	4	Table Mountain	14	—	—	—	—	—	—	0.01	7.1	9.4	85.7	2.01	28.6	0.21	21.4	0.17	14.3
		Upuma	17	—	—	—	—	—	—	—	—	3.1	52.9	3.14	76.5	0.09	29.4	0.21	23.5
Foothill Soft Bottom	4	Natal Estates Fair View	2	—	—	—	—	—	—	—	—	1.5	50.0	9.95	100.0	—	—	—	—
				No stony bottom.															

5. The distribution of the associations of stony bottom Ephemeroptera in the Umgeni River can be summarized as follows :

Afronurus oliffi association : Restricted to the head of the upper foothill torrent zone at Ross' Farm. Members of this association have their highest average incidences at the source and at Ross' Farm.

The association is composed of the following Ephemeroptera : *Afronurus oliffi, Aprionyx tricuspidatus, Castanophlebia calida, Adenophlebia sylvatica, Baetis cataractae, Baetis monticola, Centroptilum* near *excisum.*

Afronurus barnardi association : Overlapping association 1 at Ross' Farm but with a comparatively more extended distributional range which normally stretched from Ross' Farm to Dargle Forestry. Some species of this association however, tail off at Albert Falls, at the mountain torrent zone 4 of the rejuvenated river. These species can always be recognized as belonging to association 2 from the circumstances that their highest average and individual incidences occur in the mountain and foothill torrent zones.

This association comprises *Afronurus barnardi, Adenophlebia auriculata, Centroptilum sudafricanum, Centroptilum* sp. 2, *Centroptilum parvum, Baetis natalensis* and *Oligoneuriopsis lawrencei.*

Table 15

Longitudinal (downstream) distribution of the Baetidae : the genera Centroptilum and Centroptiloides.

Physical Zones	*Microprofile*	*Sqmpling Localities*	N	*Species of Centroptilum and Centroptiloides*											
				Centroptilum near *excisum*		*Centroptilum sudafricanum*		*Centroptilum parvum*		*Centroptilum* sp. 2		*Centroptilum indusii*		*Centroptilum* sp. 3	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	3.65	100.0	5.05	50.0	—	—	—	—	—	—	—	—
Mountain Torrent	1	Ross' Farm	14	1.40	31.3	4.9	57.1	—	—	1.51	28.6	0.03	6.7	—	—
Foothill Torrent	1	Dargle Police Station	2	—	—	7.8	100.0	11.6	100.0	—	—	—	—	—	—
Mountain Torrent	2	Dargle Forestry	20	—	—	14.3	80.0	0.12	15.0	0.27	35.0	0.40	30.0	0.79	15.0
Foothill Torrent	2	Watersmeet	6	—	—	—	—	—	—	—	—	—	—	—	—
		Fern Hill Flats	7	—	—	0.5	28.6	—	—	0.19	28.6	0.10	28.6	—	—
Mountain Torrent	3	Midmar	11	—	—	2.9	90.0	p[1]	—	—	—	0.55	27.3	—	—
		Morton's Drift	8	—	—	0.1	12.5	1.59	75.0	0.15	25.0	0.1	12.5	0.99	37.5
Mountain Torrent	4	Albert Falls	19	—	—	<0.01	10.5	0.02	5.3	0.04	15.8	2.89	10.5	0.44	42.1
Foothill Torrent	4	Table Mountain	14	—	—	<0.01	7.1	—	—	<0.01	7.1	0.25	7.6	—	—
		Upuma	17	—	—	—	—	—	—	0.03	5.9	0.04	5.9	—	—
Foothill Soft Bottom	4	Natal Estates Fair View	2	—	—	—	—	—	—	—	—	—	—	—	—
				No stony bottom.											

Table 15 (*continued*)

Longitudinal (downstream) distribution of the Baetidae : the genera Centroptilum and Centroptiloides.

Physical Zones	*Microprofile*	*Sampling Localities.*	N	*Species of Centroptilum and Centroptiloides*									
				Centroptilum medium		*Centroptiloides bifasciata*		*Centroptilum varium*		*Centroptilum flavum*		*Centroptilum* sp. 1	
				$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.	$\bar{x}$	% pos.
Source	1	Umgeni Sponge	2	—	—	—	—	—	—	—	—	—	—
Mountain Torrent	1	Ross' Farm	14	—	—	0.03	14.3	0.02	7.1	—	—	—	—
Foothill Torrent	1	Dargle Police Station	2	0.2	50.0	0.05	50.0	0.05	50.0	—	—	—	—
Mountain Torrent	2	Dargle Forestry	20	1.04	25.0	0.19	30.0	0.01	5.0	—	—	—	—
Foothill Torrent	2	Watersmeet	6	—	—	0.13	16.7	0.03	16.7	—	—	—	—
		Fern Hill Flats	7	—	—	0.06	28.6	0.06	14.3	—	—	—	—
Mountain Torrent	3	Midmar	11	0.89	27.3	0.16	18.2	0.1	9.1	—	—	—	—
		Morton's Drift	8	3.80	37.5	0.44	50.0	1.54	37.5	—	—	—	—
Mountain Torrent	4	Albert Falls	19	0.12	10.5	0.07	26.3	—	—	<0.01	5.3	p[2]	—
Foothill Torrent	4	Table Mountain	14	0.03	7.1	0.01	12.5	0.12	21.4	—	—	0.36	7.1
		Upuma	17	0.05	11.8	0.03	5.9	0.27	23.5	—	—	0.37	11.8
Foothill Soft Bottom	4	Natal Estates Fair View	2	—	—	—	—	1.50	50.0	—	—	0.95	100.0
				No stony bottom.									

[1] *Centroptilum excisum* not included.

[2] present but not recorded from survey samples.

Afronurus scotti association : This association, to which *Afronurus scotti* belongs, is the most widespread of all the species of the genus. It overlaps associations 1 and 2 in the mountain torrent zone 1 on one hand and, with association 4, in the mountain torrent zone 4 on the other hand. Characteristic of this association is its predominance between the mountain torrent zones 2 and 4 (Dargle Forestry — Albert Falls). It includes *Afronurus scotti*, *Choroterpes (Euthraulus)? bugandensis*, *Baetis harrisoni*, *Centroptilum indusii*, *Centroptilum* sp. 3, *Centroptilum medium*, *Centroptiloides bifasciata*, *Neurocaenis discolor*, *Prosopistoma* sp. and *Elassoneuria trimeniana*.

Afronurus peringueyi association : This association is largely confined to the river in the mountain and foothill torrent zones 4. Some members of this association penetrate upstream into the mountain torrent zone 3. The highest average numbers of species of this association occur between Albert Falls and Upuma, mountain and foothill torrent zone 4. The species

Table 16

Arrangement of Ephemeroptera in Umgeni according to associations

Each value indicates the highest percentage incidence of a particular species among all macro-invertebrates per sample from all samples collected at a specific locality. [Symbols denote the following : B = backwaters; F = flats; R = runs; S = stickles; C = cascades.]

	Species and Their Associations.	*Altitude in feet*	6000 - 6500	5000 - 6000	4000 - 5000	3000 - 4000	3000 - 4000	3000 - 4000	3000 - 4000	2000 - 3000	2000 - 3000	1000 - 2000	0 - 1000	0 - 500
		Locality.	Umgeni Sponge	Ross's Farm	Dargle Police Station	Dargle Forestry	Watersmeet	Fern Hill Flats	Midmar (Howick)	Morton's Drift	Albert Falls	Table Mountain	Upuma	Natal estates
Association 1	*Baetis monticola* CRASS		—	19.3 S	—	—	—	—	—	—	—	—	—	—
	Pseudocloeon inzingae CRASS		—	17.6 P	—	—	—	—	—	—	—	—	—	—
	Afronurus oliffi SCHOONBEE		—	13.3 P	—	—	—	—	—	—	—	—	—	—
	Aprionyx tricuspidatus CRASS		0.7 F	5.2 F	—	—	—	—	—	—	—	—	—	—
	Castanophlebia calida BARNARD		0.7 F	9.1 S	—	—	—	—	—	—	—	—	—	—
	Baetis cataractae CRASS		—	0.7 S	—	0.3 F	—	—	—	—	—	—	—	—
	Centroptilum near *excisum* BARNARD		4.4 F	11.7 B	—	—	—	—	—	—	—	—	—	—
	Adenophlebia sylvatica CRASS		13.0 F	11.3 P	—	0.2 F	—	—	—	—	—	—	—	—
Association 2	*Adenophlebia auriculata* EATON		14.4 F	21.1 P	0.8 S	17.4 SR	—	—	3.6 F	—	—	—	—	—
	Afronurus barnardi SCHOONBEE		—	4.3 P	—	5.6 P	—	—	1.8 S	0.9 S	P R	—	—	—
	Centroptilum sudafricanum LESTAGE		10.1 F	15.3 B	8.2 R	65.8 B	—	1.8 R	13.3 F	1.1 R	0.5 F	PRS	—	—
	Centroptilum sp. 2		—	16.7 P	—	1.6 P	—	1.0 RS	—	0.8 R	0.5 SC	P S	0.5 RS	—
	Baetis natalensis CRASS		—	14.5 S	2.6 S	39.1 S	2.2 R	0.8 RS	2.4 S	8.4 RS	1.2 RS	0.1 S	—	—
	Centroptilum parvum CRASS		—	—	16.7 R	1.1 P	—	—	—	3.2 RS	0.3 F	—	—	—
	Oligoneuriopsis lawrencei CRASS		—	—	1.8 R	—	0.5 R	3.0 R	6.3 S	—	0.2 S	3.6 S	—	—

comprising it are *Afronurus peringueyi, Baetis glaucus, Pseudocloeon maculosum, Centroptilum* sp. I, *C. flavum*, the baetid with ventral addominal gills, *Prosopistoma crassi and Lithogloea* near *harrisoni.*

Although the above-mentioned associations are defined primarily by reference to the distribution of the stony bottom Ephemeroptera, there are definite indications that the distribution of the remaining fauna also fits into this scheme.

On the evidence obtained, namely that several associations of the macroinvertebrate fauna occur over the length of the Umgeni each of which predominated in the various stretches of the

Table 16 *(continued)*

Arrangement of Ephemeroptera in Umgeni according to associations

Each value indicates the highest percentage incidence of a particular species among all macro-invertebrates per sample from all samples collected at a specific locality. [Symbols denote the following : B = backwaters; F = flats; R = runs; S = stickles; C = cascades.]

	Species and Their Associations.	*Altitude in feet*	6000 - 6500	5000 - 6000	4000 - 5000	3000 - 4000	3000 - 4000	3000 - 4000	3000 - 4000	2000 - 3000	2000 - 3000	1000 - 2000	0 - 1000	0 - 500
		Locality.	Umgeni Sponge	Ross's Farm	Dargle Police Station	Dargle Forestry	Watersmeet	Fern Hill Flats	Midmar (Howick)	Morton's Drift	Albert Falls	Table Mountain	Upums	Natal estates
Association 3	*Centroptiloides bifasciata* (E.-P.)		—	0.2 C	0.1 R	1.7 S	0.8 RS	0.2 R	1.2 S	1.7 S	0.5 SC	P S	0.5 RS	—
	Choroterpes (E.) ? bugandensis (KIMMINS)		—	4.4 RS	0.6 S	14.1 P	0.8 P	0.9 R	15.3 F	10.1 P	7.5 F	10.2 F	2.3 R	—
	Afronurus scotti SCHOONBEE		—	1.4 P	2.7 R	23.9 P	—	1.4 R	17.4 R	19.4 P	12.8 S	20.6 S	2.1 R	—
	Baetis harrisoni BARNARD		1.4 F	31.5 RS	25.2 S	63.0 R	23.7 RS	20.4 RS	21.5 R	39.2 RS	42.9 S	38.2 S	15.3 RS	3.1 RS
	Centroptilum varium CRASS		—	0.3 S	0.1 R	0.2 F	—	0.4 RS	1.2 S	9.9 S	—	1.2 S	3.0 RS	3.1 RS
	Neurocaenis discolor (BURMEISTER)		—	12.4 S	9.8 S	19.4 R	15.2 RS	11.3 R	32.4 RS	7.9 RS	4.7 S	7.4 S	14.2 R	3.1 RS
	Prosopistoma sp. 1		—	—	0.3 R	1.5 R	0.3 P	0.2 R	—	0.7 P	0.8 R	2.6 F	1.8 F	—
	Centroptilum sp. 3		—	—	—	8.8 P	—	—	—	5.4 P	3.3 R	—	—	—
	Centroptilum medium CRASS		—	—	0.4 S	8.2 P	—	—	5.8 S	21.6 P	2.1 F	0.4 P	0.6 RS	—
	Centroptilum indusii CRASS		—	0.5 P	—	2.4 P	—	0.7 RS	2.4 F	0.8 R	54.8 F	3.2 P	0.6 R	—
Association 4	*Baetis glaucus* AGNEW		—	—	0.1 R	1.3 R	—	—	7.0 S	3.7 R	5.7 R	17.6 RS	7.9 RS	18.8 RS
	Prosopistoma crassi GILLIES		—	—	—	—	—	—	0.4 F	0.3 RS	—	6.3 P	1.9 RS	—
	Elassoneuria trimeniana (MACLACHLAN)		—	—	—	—	—	4.5 RS	0.9 S	—	0.7 F	0.2 RS	1.5 R	0.3 RS
	Ephoron savigni (PICTET)		—	—	—	—	—	—	0.2 F	—	0.8 SC	—	—	—
	Pseudocloeon maculosum CRASS		—	—	—	—	—	—	1.8 S	0.3 P	1.9 F	1.7 RS	0.5 F	—
	Centroptilum flavum CRASS		—	—	—	—	—	—	—	—	P RS	—	—	—
	Lithogloea near *harrisoni* BARNARD		—	—	—	—	—	—	—	—	2.4 F	P F	0.8 S	—
	Baetid with ventral abdominal gills		—	—	—	—	—	—	—	—	0.3 SC	1.2 S	1.7 RS	—
	Centroptilum sp. 1		—	—	—	—	—	—	—	—	P S	5.0 S	5.0 RS	1.6 RS
	Afronurus peringueyi (E.-P.)		—	—	—	—	—	—	—	—	7.6 R	34.9 P	2.0 RS	—

river, it was assumed that the highest incidences of members of each faunal association would be shown more clearly if the highest percentage incidences for each species at each locality is taken and plotted irrespective of the season in which the collections were made. This assumption is correct if the highest incidences for the species representing each association are found to occur in the same region of the river. Table 16 is the outcome of this effort. These results clearly show regions within each association where the highest numbers of Ephemeroptera occurred in comparison with the rest of the macro-invertebrate fauna. From Table 16 the centre portions from where the different associations radiate upstream and downstream are :

Association 1 : Ross' Farm (Mountain Torrent zone 1).

Association 2 : Ross' Farm — Dargle Forestry (Mountain Torrent zone 1 — Mountain Torrent zone 2).

Association 3 : Midmar — Table Mountain (Mountain Torrent zone 3 — Foothill Torrent zone 4).

Association 4 : Albert Falls — Upuma (Mountain Torrent zone 4 — Foothill Torrent zone 4).

Discussion

Harrison and Elsworth (1958), based their subdivision into zones of the Great Berg River primarily upon its physical characteristics, since they found (p. 138), «...that the zonation of the fauna followed the same pattern (p. 170) ... it was not necessary to use the fauna to define ecological boundaries as the biotopes could already be defined in physical terms."

Oliff (1960), who also employed a physical system of zonation for the Tugela River, Natal, came to a similar conclusion as Harrison & Elsworth (1958), p. 324 : "A clear difference was found between the communities of the upper river zones and those of the other zones which comprise the greater part of the river. This difference was distinct both in the rapids and marginal vegetation." Oliff further pointed out that the species composition of the upper river zones also differed sharptly amongst themselves, even though the zones were comparatively short.

Allanson (1961), in his investigations into the ecology of the Jukskei-Crocodile River System, subdivided the Jukskei River into reaches by taking the distance which the river flowed between consecutive 500 feet contour lines as one reach. He equated these reaches with Harri-Harrison & Elsworth's (1958) foothill stony run zones (p. 61); "The Jukskei-Crocodile river system was defined as an extended hard bottom stony run zone of the lower foothill type (Harrison's zone III B). As a result its fauna was expected to show similarities to equivalent portions of either the Berg or Tugela Rivers."

From the abovementioned statements by Harrison and Elsworth (1958), Oliff (1960) and Allanson (1961) it is important to note that these authors agree with one another namely that a system of river zonation based upon physical characteristics not only reflects, but in fact determines, the biological zonation and consequently the ecological boundaries of successive faunal communities in streams. The findings of the author not only differ from those of the authors mentioned above but in some ways contradict their assumption that the physical and the biological zonations follow the same pattern.

It was on the evidence of the faunal associations and of the distribution of *Afronurus oliffi*, *Afronurus barnardi*, *Afronurus scotti* and *Afronurus peringueyi* that the genus *Afronurus* Lestage was revised. It was also on this evidence and the belief in the existence of these associations in the rivers of South Africa that the author travelled for more than a thousand

miles in 1962 to the Cape to collect for the first time in the Great Berg River System more than twenty specimens of *Afronurus barnardi* (= *A. harrisoni* forma minor, BARNARD, 1932) the existence of which was not recorded until that date.

RÉSUMÉ

Le rôle de l'écologie dans la détermination des espèces du genre *Afronurus* LESTAGE (Heptageniidae) en Afrique du Sud.

La rivière Umgeni, Natal, Afrique du Sud, parcourt 145 miles de sa source située à une altitude de 6000 pieds, à son embouchure dans l'océan indien au nord de Durban. Des recherches hydrobiologiques ont été effectuées sur cette rivière, ayant pour but le cumul des données de base nécessaires à la détermination de taux d'effluents standards pour la protection de la qualité des eaux. La faune d'éphémères peuplant les fonds rocheux a été choisie pour illustrer la zonation de la rivière, en raison de la dominance de ceux-ci sur les autres groupes de macro-invertébrés et de leur sensibilité à la pollution. Utilisant les définitions de ALLEN (1951) et HARRISON et ELSWORTH (1958), les habitats de fonds de rivière suivants ont été étudiés : back waters (portion de la rivière en dehors du courant principal), pools (bassins), flats (section de rivière peu profonde et de courant faible), runs (section de rivière de courant fort), stickles (rapides), et cascades. Des données sur les préférences en habitat de chaque espèce sont données (Tableaux 4-9) ainsi que la distribution des espèces le long de la rivière (Tableaux 10-15). Dans les tableaux 4-15, N = le nombre d'échantillons; $\bar{x}$ = le nombre moyen de spécimens par échantillon (N); et % pos. = le pourcentage d'échantillons dans lesquels l'espèce a été trouvée. Dans le Tableau 16 les espèces sont arrangées de façon à montrer les associations. Pour illustrer ces associations on se sert du plus fort pourcentage d'incidence d'une espèce parmi tous les échantillons dans une localité, quelle que soit la saison (de préférence à une moyenne saisonnière). Les résultats se sont avérés très semblables pour d'autres invertébrés. La zonation de la rivière Umgeni diffère de celle des autres rivières sud-africaine, comme l'ont mentionné d'autres auteurs.

ZUSAMMENFASSUNG

Die Rolle der Ökologie in der Artabschätzung der Gruppe *Afronurus* LESTAGE (Heptageniidae) in Südafrika.

Der Umgeni Fluss in Natal, Südafrika, fliesst 145 Meilen von seinem Ursprung von einer Höhe über 6000 Füsse zum Indischen Ozean nördlich von Durban. Hydrobiologische Studien wurden von diesem Fluss gemacht mit dem Ziel grundlegende Daten zu sammeln, welche für die Formulierung von Ausflussrichtmassen zur Wasserqualitätsbeschützung nötig sind. Die Fauna der Ephemeroptera von steinigen Böden war, um die Flusszone zu illustrieren, gewählt worden, weil Ephemeroptera, die dominierende macrowirbellose Gruppe ist, und weil diese sehr empfindlich für Verunreinigung ist. Bei Verwendung der Definitionen von ALLEN (1951) und HARRISON & ELSWORTH (1958) wurden folgende Flussbodenhabitate studiert : Hinterflüsse, Tümpel, ebenfliessend, fliessend, fliessend und fallend ("stickels"), und Wasserfälle. Daten an Heimatbevorzugung aller Flussarten ist gegeben (Tabelle 4-9) und die Längengrad-Verteilung aller Arten im Fluss ist auch präsentiert (Tabelle 10-15). In Tabellen 4-16 : N = die Nummer der gesammelten Proben; $\bar{x}$ = die durchschnittliche Zahl von Individuen pro Probe (N); und

% pos. = der Prozentsatz von Proben (N) in welchen die Art gefunden wurde. In Tabelle 16 sind die Arten arrangiert um die Assoziation zu zeigen. Der höchste Ausbreitungs-Prosentsatz von einer Art unter allen Proben von einer Gegend, ohne Rücksicht auf die Jahreszeit (vorzugsweise als Jahresdurchschnitt) sind gebraucht, um die Assoziation darzustellen. Ergebnisse waren ähnlich für andere wirbellose Tiere. Die Zone des Umgeni Flusses unterscheidet sich von anderen südafrikanischen Flüssen, wie andere Autoren berichteten.

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